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Effects of invasive *Rosa rugosa* on Baltic coastal dune communities depend on dune age

Marcin W. Woch[1], Paweł Kapusta[2], Małgorzata Stanek[2], Katarzyna Możdżeń[3], Irena M. Grześ[4], Elżbieta Rożej-Pabijan[5], Anna M. Stefanowicz[2]

1 *Institute of Biology, Nicolaus Copernicus University in Toruń, Lwowska 1, PL-87-100, Toruń, Poland* **2** *Władysław Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, PL-31-512, Kraków, Poland* **3** *Unafiliated, Kraków, Poland* **4** *Department of Zoology, Faculty of Biology and Biotechnology, University of Warmia and Mazury, Oczapowskiego 5, PL-10-719, Olsztyn, Poland* **5** *Institute of Biology, Pedagogical University of Kraków, Podchorążych 2, PL-31-054, Kraków, Poland*

Corresponding author: Paweł Kapusta (p.kapusta@botany.pl)

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Abstract

Rosa rugosa Thunb. (Japanese Rose) is one of the most invasive species in Europe. It spreads spontaneously in coastal areas of western, central and northern Europe, posing a threat to dune habitats, including those indicated in the EU Habitats Directive as particularly valuable. *R. rugosa* has already been reported to displace native plants and alter soil properties. However, little is known about how these effects are mediated by the habitat context or the invader condition (health, ontogenetic stage). This study addressed that gap by examining vegetation and soil in 22 *R. rugosa*-invaded sites, half of which were in yellow dunes and the other half in grey dunes, i.e. two habitats representing the earlier and later stages of dune succession. The study was conducted on the Hel Peninsula (Poland's Baltic coast). *R. rugosa* had a significant impact on dune vegetation, but the impact was strongly dependent on the habitat type. In the yellow dune sites, *R. rugosa* outcompeted most resident plant species, which translated into a strong decline in their total cover and richness. The invasion was almost not accompanied by changes in soil properties, suggesting that it affected the resident vegetation directly (through space takeover and shading). In the grey dunes, *R. rugosa* caused a shift in species composition, from that characteristic of open communities to that typical of forests. In this habitat, a significant increase in the soil organic layer thickness under *R. rugosa* was also observed, which means that both direct and indirect effects of the invasion on the vegetation should be assumed. Finally, a negative relationship was found between the total chlorophyll content in *R. rugosa*

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leaves and the parameters of resident plant communities, showing that the invasion effects can vary not only across habitats, but also with the condition of the invader. The results may have practical implications for managing *R. rugosa* invasions in coastal sand dune systems. Since *R. rugosa* accelerates grey dune succession, protecting this habitat may be more urgent and, at the same time, more complicated than protecting dunes at the earlier stages of development.

Keywords
ecological succession, functional trait, grey dune, plant invasion, soil property, species composition, species richness, yellow dune

Introduction

Rosa rugosa Thunb. (Japanese Rose) is a rhizomatous multi-stemmed erect deciduous shrub. The plant is native to northern Japan, the Korean Peninsula, north-east China and the Russian Far East, where it is an essential component of coastal vegetation, such as pioneering communities of sand dunes and rocky and shingle shores, as well as species-rich meadows (Bruun 2005). In China and Japan, *R. rugosa* is considered endemic. In these countries, it is a Red-book species and is legally protected due to a rapid decline in the number of populations caused by anthropogenic pressure (Yang et al. 2009; Nakata et al. 2018). Beyond its native range, *R. rugosa* shows great expansion capacity and has been identified as one of the primary invasive problems in many regions of the world (CABI 2022).

In NW Europe, *R. rugosa* is ranked amongst the seven worst invasive plants (Dassonville et al. 2008). It was originally introduced at the end of the 18th century as a crop and ornamental plant and in the 20th century, it was widely used to stabilise the dunes (Isermann 2008b). It naturalised at the beginning of the 20th century and began to spread spontaneously mainly along sea coasts, becoming widely present between latitudes of 46° and 68° (Bruun 2005). It generally establishes on coastal sand dunes, where it tends to form extensive and impenetrable monodominant thickets that displace local vegetation with high conservation status (Bruun 2005; Isermann 2008b; Kunttu and Kunttu 2017; Perzanowska and Korzeniak 2020) and change the physicochemical properties of the soil and the structure of soil microbial communities (Vanderhoeven et al. 2005; Stefanowicz et al. 2019). Counteracting the *R. rugosa* invasion is a challenge due to the plant's remarkable ability to regenerate after disturbances, such as being buried with sand, uprooted or burned and high resistance to environmental stresses, including drought, frost and salinity (Belcher 1977; Bruun 2005; Kollmann et al. 2011).

Many years of studies have resulted in a good understanding of *R. rugosa* ecology in the areas of invasion. However, there are still gaps in this knowledge. Amongst other things, it is unclear whether and how the influence of *R. rugosa* on local vegetation and soil is modified by the ecological and environmental context. The coastal sand dune systems on which this study focuses are highly heterogeneous as they include dunes

at different stages of maturity – from unstable dunes (yellow dunes) to semi-fixed and fixed dunes (grey and brown dunes) (McLachlan and Defeo 2018). *R. rugosa* enters all types of dunes (Kollmann et al. 2007; Isermann 2008a), which means that it invades plant communities representing all stages of dunes' ecological succession. As these communities obviously differ in species composition and, consequently, in the composition of plant functional traits, they may respond differently to the invasion. There were few attempts to verify this hypothesis and they brought inconclusive results (Isermann 2008b; Thiele et al. 2011). Isermann (2008b) studied the effects of *R. rugosa* on local vegetation depending on its type and showed that the cover and species richness of herbaceous plants (in particular, those typical of coastal grasslands) decreased with the increase of the invader cover and this decrease was stronger in yellow and grey dune communities (i.e. in earlier succession stages) in comparison to brown dune communities. However, the differences in the strength of the revealed relationships were not statistically checked. Additionally, little was said about the nature of invasion-induced changes in the species composition of the studied types of communities. Thiele et al. (2011) investigated the effect of three invasive plants, *Heracleum mantegazzianum*, *Lupinus polyphyllus* and *R. rugosa*, on plant species richness and found that this effect interacted with the type of habitat (or the type of invaded community) for *L. polyphyllus*, but not for the other two species, including *R. rugosa*.

The response of local vegetation to the alien plant invasion may depend on the functional traits of the resident plants, but also on how they interact with the functional traits of the invader (Helsen et al. 2021; Kaushik et al. 2022). Unstable dunes where primary succession takes place are colonised by plant species adapted to hostile environments. Resistance to environmental stresses is important there, while interspecific competition plays a minor role (Olff et al. 1993; Callaway and Walker 1997). *R. rugosa* has both the properties of pioneering species and great ability to compete for space and other resources. Therefore, it is possible that entering the fragile pioneering communities, it displaces the resident plants much easier than in the case of communities of further stages of succession, where interspecific competition is inherently more intense. This conclusion can be drawn from the competitive hierarchy theory, according to which the chance of species co-existence is positively correlated with their functional similarity and, hence, the similarity of their competitive abilities (Fried et al. 2019).

Invasive species affect local vegetation not only directly, but also indirectly by transforming habitat conditions. Those that are capable of creating ecological niches for new species of plants and animals are called invasive ecosystem engineers or transformers (Richardson et al. 2000; Fei et al. 2014). Amongst them are species associated with coastal ecosystems, for example, *Ammophila arenaria*, invasive in North America (Pickart 2021), *Lupinus nootkatensis*, invasive in Iceland (Vetter et al. 2018) and *Senecio inaequidens*, invasive in Europe (Van De Walle et al. 2022). By stabilising the ground surface and producing substantial amounts of organic matter, these invaders accelerate the soil formation process. *R. rugosa* appears to be such a transformer species. First, it can quickly produce a dense cover over a large area (due to the ease of clonal reproduc-

tion) (Kollmann et al. 2009), which effectively limits the mobility of dunes. Second, it is a phanerophyte, i.e. a plant with persistent and relatively high aboveground parts. As such, it can form a canopy that significantly reduces insolation – an important parameter in the coastal environment (Olff et al. 1993) – of the herbaceous layer in which most of the resident dune species occur. Third, it produces considerable amounts of leaf litter (Stefanowicz et al. 2019), which may be a source of limiting nutrients. Putting it all together, invasive *R. rugosa* can be regarded as a transformer leading to acceleration of dune succession. It can also be hypothesised that this role is limited to the early succession stages where sand immobilisation, shading and nutrient supply are potentially of greatest importance for plant colonisation.

Perennial woody plants show the ontogenetic variation that extends over many years. They gradually develop from seedling through the reproductive and ageing stages until they finally begin to die. Along with the successive stages of development, the appearance and vigour of individuals change and, thus, their interaction with other community members (Boege and Marquis 2006; Staska et al. 2014; Lundgren and Des Marais 2020; Qiu et al. 2021). Invasive *R. rugosa* seems to be no exception in this respect. During the fieldwork, we repeatedly observed that some *R. rugosa* patches had a higher ratio of dead to living shoots and, thus, more sparse foliage than others, which appeared to be related to their advanced ontogenetic stage. Perhaps the weakened competitive pressure in such patches opens the way for species previously displaced by the invader to return or for new species to establish.

This study checked whether: 1) the impact of invasive *R. rugosa* on the Baltic coastal dune communities and soils depends on the ecological context, more precisely on the stage of dune succession and whether: 2) the invaded vegetation responds to the ontogenetic variation of the invader. To achieve the study objectives, four types of plots – established in *R. rugosa* patches and adjacent patches of non-invaded local vegetation in both yellow and grey dune sites – were compared in terms of resident plant community parameters (total cover, species richness and composition, functional trait diversity) and soil physicochemical properties. In addition, the surveyed *R. rugosa* patches were described with a number of variables presumably related to the ontogenetic stage or health condition of the invader, including cover, percentage of dead shoots, the content of chlorophyll (Tamary et al. 2019; Zhang et al. 2022) and phenolics in leaves (Borges et al. 2013; Tuominen and Salminen 2017), which were then used to explain coverage, richness and species composition of resident plants.

Methods

Study area and sampling

The study area was the Hel Peninsula (northern Poland). It is a narrow (200–3000 m wide) and very elongated (36 km long) spit separating the Bay of Puck from the Baltic Sea (Fig. 1). The Peninsula is one of the geologically youngest parts of the Polish coast. It formed between 6900 and 1000 years ago from Holocene siliciclastic sediments

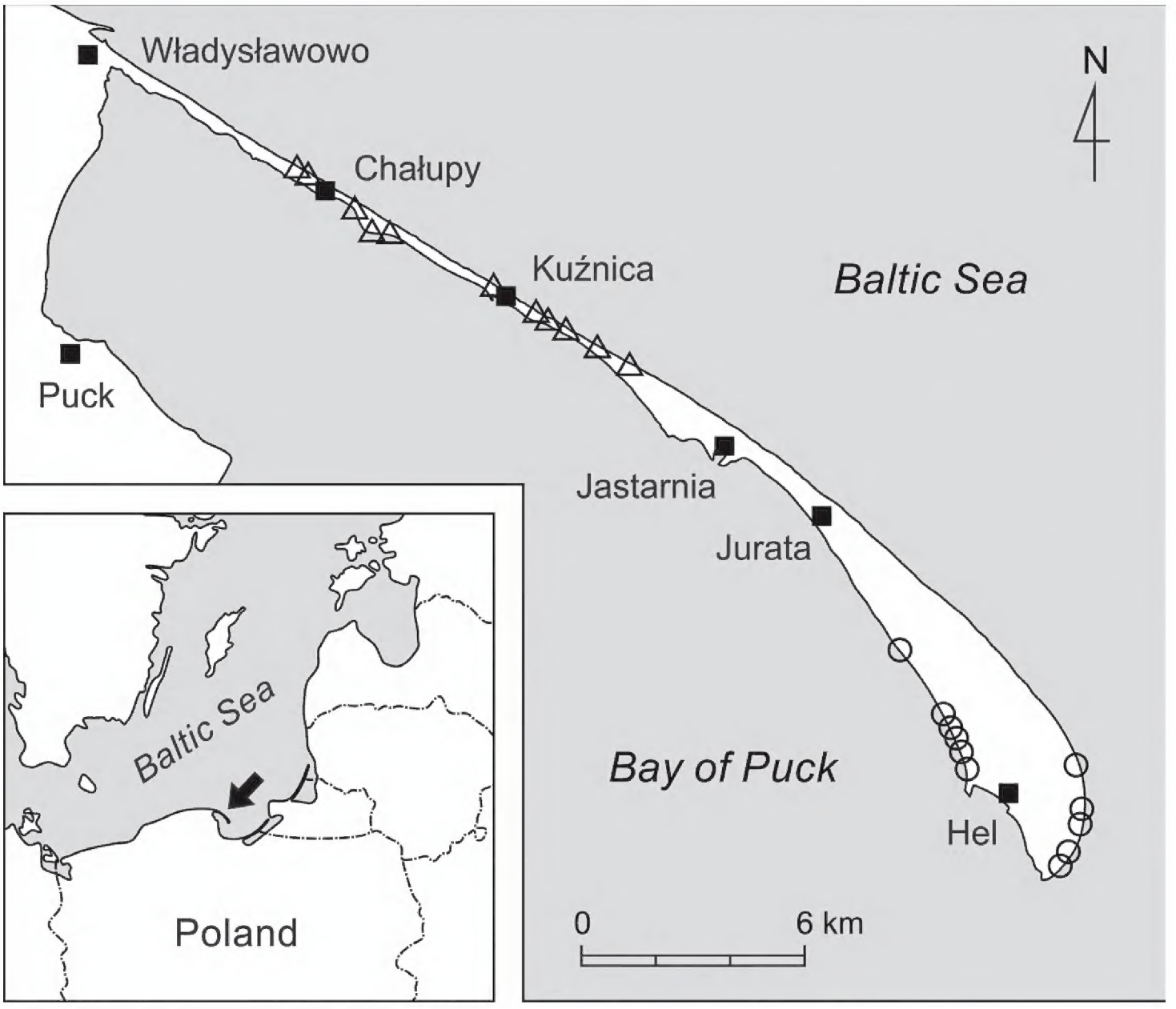

Figure 1. Study area and study sites in four locations: near the villages of Chałupy and Kuźnica and to the west and east of the town of Hel; triangles – yellow dune sites, circles – grey dune sites, black squares – towns and villages.

(mainly sand, less gravel) deposited on the Cretaceous formations by the sea current (Tomczak 1995). The thickness of these sediments reaches 100 m. The relief of the area is nearly level to gently undulating. Its main elements are aeolian dunes, the height of which varies mostly between 3 and 5 m, rarely exceeding 10 m (the maximum height is 22.5 m). Most soils that develop on them are classified as Arenosols (on dunes with unconsolidated or partly consolidated material) and Podzols (on dunes stabilised by forest vegetation) according to the IUSS Working Group WRB (2015). There is no watercourse network, but there are small depressions with periodically wet conditions. The Hel Peninsula lies in the transitional climate zone (shaped by oceanic and continental influences) and has a coastal climate with mild winters and summers. The growing period lasts about 210 days. The average annual temperature is about 9.0 °C. In a year, the rainfall is ca. 750 mm.

The Hel Peninsula is largely covered by the Scots pine and crowberry sub-Atlantic forests of the *Empetro nigri-Pinetum* (Libb. and Siss. 1939 n.n.) Wojt. 1964 association. Between the forest area and the shoreline, there are often zonal strips of loose

shrublands from the *Salicion arenariae* R. Tx. 1952 alliance (the *Rhamno-Prunetea* Rivas Goday and Garb. 1961 class), followed by grassland vegetation typical of the dunes of the sub-Atlantic Central European coastal region. The latter is represented mainly by two communities representing the earlier and later succession stages: 1) tall-grass perennial swards of the *Elymo-Ammophiletum* association Br.-Bl. and De Leeuw 1936 (the *Ammophiletea* Br.-Bl. and R. Tx. 1943 class), hereinafter referred to as the yellow dune community/vegetation and 2) tussock grasslands of the *Helichryso arenarii-Jasionetum litoralis* Libb. 1940 association (the *Koelerio glaucae-Corynephoretea canescentis* Klika in Klika and Novak 1941 class), hereinafter referred to as the grey dune community/vegetation. Both these communities were included in this study as they are most endangered due to the invasion of *R. rugosa*.

The study was conducted in 22 sites established in four different locations: near the villages of Chałupy (n = 5) and Kuźnica (n = 6) and to the west (n = 5) and east (n = 6) of the town of Hel (Fig. 1). The sites were selected so as to include a patch of invader thicket (large and dense enough; Table 1) and a patch of resident grassland vegetation adjacent to the former. One circular sample plot of 4 m^2 was established in each patch, which gives a total of 44 sample plots. The edge-to-edge distance between plots in a pair, i.e. between the invasion plot and the resident vegetation plot (control), was kept as small as possible; it ranged from two to five metres across the sites. Another criterion for selecting the sites was that they should evenly represent the two dominant types of grassland communities. Thus, 11 sites were established in the area of the occurrence of yellow dune vegetation (Chałupy and Kuźnica locations) and 11 sites were established where grey dune vegetation prevailed (Hel locations). Plant communities were identified in the field using a guide by Matuszkiewicz (2013) based on patches of vegetation not influenced by *R. rugosa*.

Botanical data and soil samples were collected at the end of May 2018. The May date was chosen because it combined the sufficient advancement of the growing season and the relatively low level of anthropogenic disturbance (eutrophication, trampling) related to tourist traffic. At each plot, all vascular plant species were identified and their cover-abundances were estimated using the seven-grade Braun-Blanquet scale: r (< 5%, one small individual), + (< 5%, one to three individuals), 1 (< 5%, several individuals), 2 (5–25%); 3 (25–50%), 4 (50–75%) and 5 (75–100%). Species nomenclature followed Mirek et al. (2002). From each plot, three samples of mineral soil were taken

Table 1. Characteristics of *Rosa rugosa* thickets (means ± standard deviations) for the yellow and grey dune sites. Note that total phenolics content was expressed as Tannic Acid Equivalent (TAE). Fv/Fm – the maximum photochemical efficiency of photosystem II (for explanation, see the text).

Variable	Yellow dune sites, n = 11	Grey dune sites, n = 11
Area (m^2)	204 ± 142	113 ± 129
Coverage (%)	92 ± 8	89 ± 6
Annual shoots (%)	6.4 ± 7.8	9.5 ± 5.2
Dead shoots (%)	6.8 ± 7.8	18.2 ± 13.5
Total chlorophyll (mg g^{-1})	1.54 ± 0.23	1.52 ± 0.15
Fv/Fm	0.753 ± 0.061	0.711 ± 0.098
Total phenolics (mg TAE g^{-1})	51.0 ± 2.0	51.2 ± 2.6

(after removal of the organic layer, if present) from a depth of 0–10 cm and bulked to obtain one composite sample. At the soil sampling spots, the thickness of the organic layer was measured and averaged over the plot. Additional work was done in the invasion plots. The percentage of annual and dead *R. rugosa* shoots was estimated. Additionally, fragments of vivid shoots with leaves were randomly collected from *R. rugosa* (from three individuals per plot) for the chlorophyll fluorescence analysis. Each fragment was wrapped with a moistened paper towel, placed in a separate plastic container and transported to the laboratory on the same day. In October 2018, senescing *R. rugosa* leaves were sampled (from three individuals per plot) for analysis of phenolics content; they were kept frozen at –20 °C until analysis.

Chlorophyll content and fluorescence analysis

The leaf content of chlorophyll was analysed according to Barnes et al. (1992). Fresh material of the *R. rugosa* leaves was extracted in dimethyl sulphoxide (SIGMA-Aldrich, St. Louis, MO, USA) at 65 °C for 12 h. The chlorophyll was measured spectrophotometrically at 648 and 665 nm with a CECIL spectrophotometer (Cambrige, United Kingdom). Its total content was calculated using the formula:

$$[(7.49 \times A_{665} + 20.34 \times A_{648}) \times V)] / (1000 \times W),$$

where A is absorbance of wavelength (nm), V is the volume of the extract (ml) and W is the weight of the sample (g).

The chlorophyll *a* fluorescence was determined with a fluorimeter (Hansatech, United Kingdom). The second leaves were acclimatised to the dark for 30 minutes using clips. After this time, leaves were exposed to excitation light (1000 μmol m^{-2} s^{-1}) for 1 s (Lichtenthaler et al. 2004). Amongst the measured parameters were: F0 – zero fluorescence, Fm – maximal fluorescence and Fv/Fm – the maximum photochemical efficiency of photosystem II (PSII), where Fv = Fm – F0.

Analysis of soil physicochemical properties

Depending on the analysed properties, the soil samples were dried either at room temperature (pH, electrical conductivity, content of $N\text{-}NH_4$, $N\text{-}NO_3$ and $P\text{-}PO_4$) or at 105 °C (organic C content and total content of N, P, Na and Ca) overnight and then sieved to 1 mm. The pH (ISO 1994) and electrical conductivity (PN-ISO 1997) were measured after dilution of soil in distilled water (1:5, w:v) using a Hach HQ40D multi-meter. For $N\text{-}NH_4$, $N\text{-}NO_3$ and $P\text{-}PO_4$ analysis, soil samples were shaken in water (1:10, w:v) for 1 h using a 358S shaker (Elan) and then passed through cellulose acetate syringe filters with a pore size of 0.45 μm (Huang and Schoenau 1998; modified). The content of $N\text{-}NH_4$ in the extracts was determined using an ion chromatograph Dionex DX-100, while that of $N\text{-}NO_3$ and $P\text{-}PO_4$ was determined using Dionex ICS-1100. The contents of elements were determined for soil samples ground

by a vibratory mill (Analysette 3 Spartan Pulverisette 0, Fritsch). Organic C content was measured with a Leco RC-612 (ISO 1995). Total N content was analysed by the Kjeldahl method, which included soil mineralisation in H_2SO_4 with Kjeltabs (K_2SO_4 + $CuSO_4 \cdot 5H_2O$; Foss Tecator Digestor Auto 20) and distillation using a Foss Tecator Kjeltec 2300 Analyser Unit (AN 300 Ver. 4.0). Prior to the determination of the total content of Ca, Na and P, soil was mineralised in suprapur $HClO_4$ (Foss Tecator Digestor Auto 40). The metals were analysed with a flame atomic absorption spectrometer (AA280FS, Varian), while P was analysed with a colorimeter (DR 3800, Hach Lange) using the vanadate-molybdate method (Nowosielski 1974).

Data handling and analysis

Each plant species recorded in this study was characterised using several categorical functional traits. They were: functional group identity (forbs, graminoids, legumes, woody plants), C-S-R life strategy, life form, seed dispersal type and pollination type (Klotz et al. 2002; Kleyer et al. 2008). For each plot, the number of species representing a given function (trait category), the total number of species (species richness) and the total plant coverage were calculated. To determine the latter variable, species cover-abundance values expressed using the seven-grade Braun-Blanquet scale were converted to equivalent percentage cover values, 1%, 2%, 3%, 13%, 38%, 63% and 88% (Tichý et al. 2020) and then summed up. Summation results often exceeded 100% due to the fact that the vegetation has a multi-layered structure. Only the resident plant species were included in the above calculations, i.e. all except *R. rugosa*. The number of endangered species (protected and/or rare), as defined by the Regulation of the Minister of the Environment of 9 October 2014 on the protection of plant species (Ministry of Environment of the Republic of Poland 2014) and the Polish Red List (Kaźmierczakowa et al. 2016), was also calculated.

Prior to statistical analysis, the data were transformed to reduce variability and approximate normality: total coverage and species richness of resident plants, *R. rugosa* thicket characteristics and soil properties were log-transformed and then normalised, while resident plant species cover-abundances and functional traits (i.e. species numbers in functional trait categories) were square-root transformed (Anderson et al. 2008). Variables carrying little information were not taken into account in multivariate analyses; these were species occurring as singletons and functional traits rarely found in the studied communities (represented by less than two species and/or absent in ≥ 75% of the study plots).

The effects of plot type (invasion vs. control plots), site type (yellow vs. grey dune sites) and the interaction of these factors on the total cover and species richness of resident plants and the number of protected plant species were determined using linear mixed-effects (LME) models. Two random factors were included in the models: site, within which plots were nested and location, within which sites were nested. The models were fitted using the "nlme" R package (Pinheiro et al. 2017) and their assumptions were checked with diagnostic tools ("plot.lme" function) provided with the package. The datasets on the plant functional traits and soil properties contained many

Table 2. Soil properties (means ± standard deviations) for the control (C) and invasion (I) plots within the yellow and grey dune sites and the effects of site type, plot type and their interaction on these properties, as shown by *F*-values derived from the LME analysis. Significant effects are marked with asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Variable	Yellow dune sites		Grey dune sites		Effects		
	C plots, n=11	I plots, n=11	C plots, n=11	I plots, n=11	Site type	Plot type	Interaction
Organic layer thickness (cm)	1.3 ± 1.2	1.7 ± 1.1	1.2 ± 0.8	2.6 ± 1.3	0.1	21.2***	7.1*
pH	6.2 ± 0.7	6.2 ± 0.6	5.5 ± 0.3	6.0 ± 0.4	1.4	11.7**	12.4**
Electrical conductivity (μS cm^{-1})	15.3 ± 4.3	13.6 ± 2.8	11.8 ± 2.8	13.4 ± 4.1	0.6	0.0	4.2
Organic C (%)	0.33 ± 0.34	0.44 ± 0.42	0.14 ± 0.14	0.20 ± 0.13	0.7	3.8	0.0
Total N (%)	0.018 ± 0.016	0.032 ± 0.032	0.009 ± 0.007	0.014 ± 0.008	0.7	4.5*	0.4
C/N	20.3 ± 28.5	22.2 ± 27.4	23.9 ± 26.5	14.0 ± 4.4	0.0	0.2	1.0
Total P (mg kg^{-1})	94 ± 45	103 ± 40	89 ± 45	57 ± 25	1.0	1.4	4.5*
Total Na (mg kg^{-1})	8.3 ± 2.6	8.7 ± 2.7	5.5 ± 1.2	4.5 ± 0.9	22.9*	1.2	3.8
Total Ca (mg kg^{-1})	339 ± 171	353 ± 146	261 ± 88	266 ± 162	1.4	0.0	0.2
$N\text{-}NH_4$ (mg kg^{-1})	0.66 ± 0.34	0.77 ± 0.42	0.65 ± 0.39	0.56 ± 0.27	3.8	0.1	1.5
$N\text{-}NO_3$ (mg kg^{-1})	0.29 ± 0.29	0.32 ± 0.39	0.10 ± 0.06	0.10 ± 0.03	0.5	0.1	0.5
$P\text{-}PO_4$ (mg kg^{-1})	1.16 ± 0.69	1.67 ± 0.85	0.91 ± 0.44	1.47 ± 0.53	0.1	25.0***	0.2

variables, to some extent correlated with each other and, therefore, they were analysed using a multivariate approach – permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA models had the same error term structure as the LME models and were based on Euclidean distances. Data on species abundances were analysed in the same way, except that Bray-Curtis distances were used. For the species data, in addition to PERMANOVA, similarity percentage (SIMPER) analysis (Anderson et al. 2008) with a 50% contribution cut-off point (Clarke 1993) was performed on the Bray-Curtis distance matrix to identify species that contributed most to the differences between invasion and control plots. To visualise the results of PERMANOVAs, principal coordinates analysis (PCoA) ordinations were generated, wherein plots were symbol-coded according to plot and/or vegetation type. Each PCoA was performed on exactly the same data as the corresponding PERMANOVA.

The variability in the total coverage of the resident plants, as well as their species richness and composition across the invasion plots, was explained using distance-based linear models (DistLM) (Anderson et al. 2008). The explanatory variables were preselected from Tables 1, 2; they were: four parameters of *R. rugosa* thickets (thicket area, percentage of annual shoots, total chlorophyll content and total phenolics content) and seven soil properties (the contents of organic C, total Na, total Ca, $N\text{-}NH_4$, $N\text{-}NO_3$ and $P\text{-}PO_4$ and the C/N ratio). Pre-selection was made on the basis of the variance inflation factor (VIF) provided with the "car" R package (Fox and Weisberg 2011) and its aim was to reduce the multi-collinearity in the explanatory dataset; VIF for the variables used in the analysis was < 4. Forward selection procedure and the AICc criterion were used to obtain the best models explaining the parameters of resident plant communities. For total coverage and species richness, DistLM was based on Euclidean distances, while, for species composition, it was based on Bray-Curtis distances. To visualise the results of DistLM for species composition, distance-based redundancy analysis (dbRDA) was used.

PERMANOVA, PCoA, DistLM and dbRDA routines were executed using PRIMER 7 with the PERMANOVA+ package (Anderson et al. 2008). Other analyses were carried out in R 3.3.3 (R Core Team 2020).

Results

A total of 55 species of resident vascular plants (i.e. other than *R. rugosa*) were found in this study, including four endangered species: *Agrostis vinealis*, *Epipactis atrorubens*, *Festuca polesica* and *Lathyrus japonicus* ssp. *maritimus*. Amongst them, there were 11 ubiquitous species, i.e. occurring in both types of sites, yellow and grey dune sites and in both types of plots, invasion and control plots (Suppl. material 1: fig. S1). There were almost twice as many species composing the yellow dune communities (44 species) as those composing the grey dune communities (25 species). The difference was more pronounced in the case of unique species, i.e. exclusive to a given type of community; there were 30 species exclusive to the yellow dune community and only 11 species exclusive to the grey dune community. The control plots did not differ much from the invasion plots in the total number of species recorded therein; the former harboured 42 species, including 16 exclusive ones, while the latter harboured 39 species, including 13 exclusive ones (for shared and exclusive species lists, see Suppl. material 1: table S1).

The number of resident plant species per plot (species richness) ranged from 2 to 13, averaging 6.9 (median = 6.5) and their total coverage varied between 8% and 209%, averaging 61.9% (median = 54.5%). Both parameters differed statistically significantly between the invasion and control plots, but only within the yellow dune sites, as evidenced by the interaction effect (site type × plot type; Table 3) and post-hoc comparisons (Fig. 2A, B). The yellow dune vegetation of the control plots was characterised by about four times higher coverage (117%) and one and half times higher species richness (9.4 species per plot) than the yellow dune vegetation of the invasion plots (30% and 6.7 species per plot). Within the grey dune sites, the vegetation of the two types of plots was similar both in terms of total coverage (49% and 51% in the control and invasion plots, respectively) and species richness (5.3 and 6.2 species per plot in the control and invasion plots, respectively).

The species composition of resident plants was also influenced by the site type × plot type interaction (Table 3). Unlike in the case of univariate parameters described above, the difference between the control and invasion plots was pronounced within the grey dune sites ($t = 3.8$, $p < 0.001$), while, within the yellow dune sites, it was on the verge of statistical significance ($t = 1.5$, $p = 0.056$). PCoA diagrams (Fig. 3A, B) and SIMPER analysis (Suppl. material 1: table S2) showed that the compositional shift from the control towards invasion plots within the grey dune sites was mainly due to a considerable decrease in the abundance (expressed in both cover and frequency; cf. Suppl. material 1: table S1) of dominant species of graminoids, *Corynephorus canescens* and *Ammophila arenaria* and an increase in the abundance of *Festuca villosa*. Similar results were obtained in the analysis of functional traits; their composition was shaped by the interaction of factors (Table 3) and a more pronounced compositional

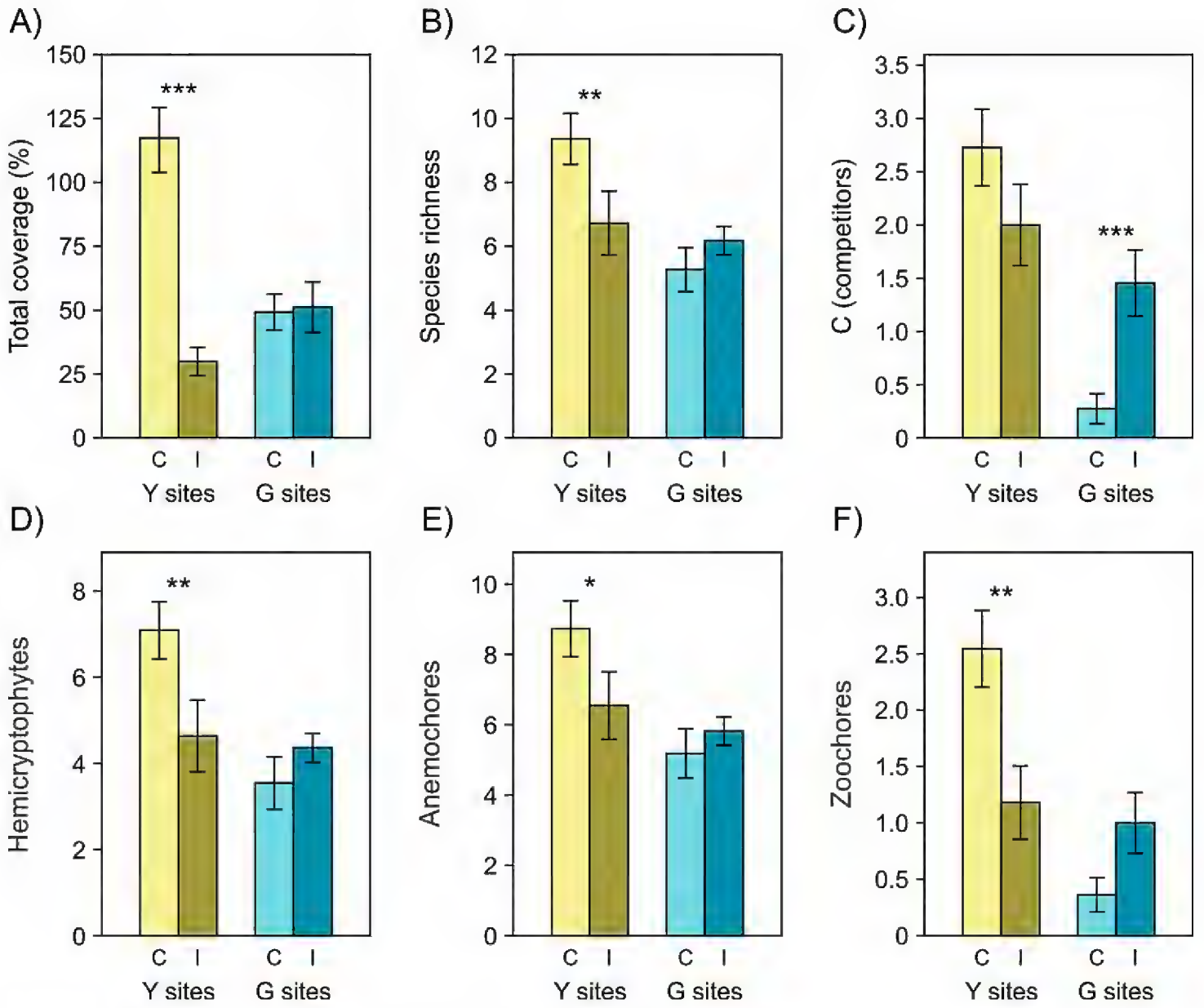

Figure 2. Means and standard errors of selected plant community parameters calculated for the C (control) and I (invasion) plots within the Y (yellow dune) and G (grey dune) sites. As a significant site type × plot type interaction effect was found for all variables (Table 3; Suppl. material 1: table S3), the differences between plot types were examined separately for the two types of sites (using Tukey's test) and marked with asterisks (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

Table 3. Effects of site type, plot type and their interaction on dune vegetation and soil, as shown by F and p values derived from the LME analysis (for univariate data; rows indicated by [L]) and pseudo-F and permutation p values derived from PERMANOVA (for multivariate data; rows indicated by [P]). Statistically significant effects are in bold.

	Site type		Plot type		Interaction	
	F	*p*	*F*	*p*	*F*	*p*
Total coverage [L]	1.1	0.4044	**29.3**	**< 0.0001**	**25.3**	**< 0.0001**
Species richness [L]	4.7	0.1633	1.5	0.2366	**8.7**	**0.0080**
Species composition [P]	2.9	0.3299	**6.5**	**0.0007**	**5.1**	**0.0011**
Functional traits [P]	3.2	0.3333	1.5	0.1852	**5.4**	**0.0016**
Soil properties [P]	1.1	0.6669	**3.2**	**0.0052**	**2.2**	**0.0399**

shift between plot types was observed within the grey dune sites (grey dune: $t = 1.9$, $p = 0.0160$; yellow dune: $t = 1.8$, $p = 0.0445$). PCoA diagrams (Fig. 3C, D) and univariate tests (Suppl. material 1: table S3; Fig. 2C–F) suggested that the differences in the

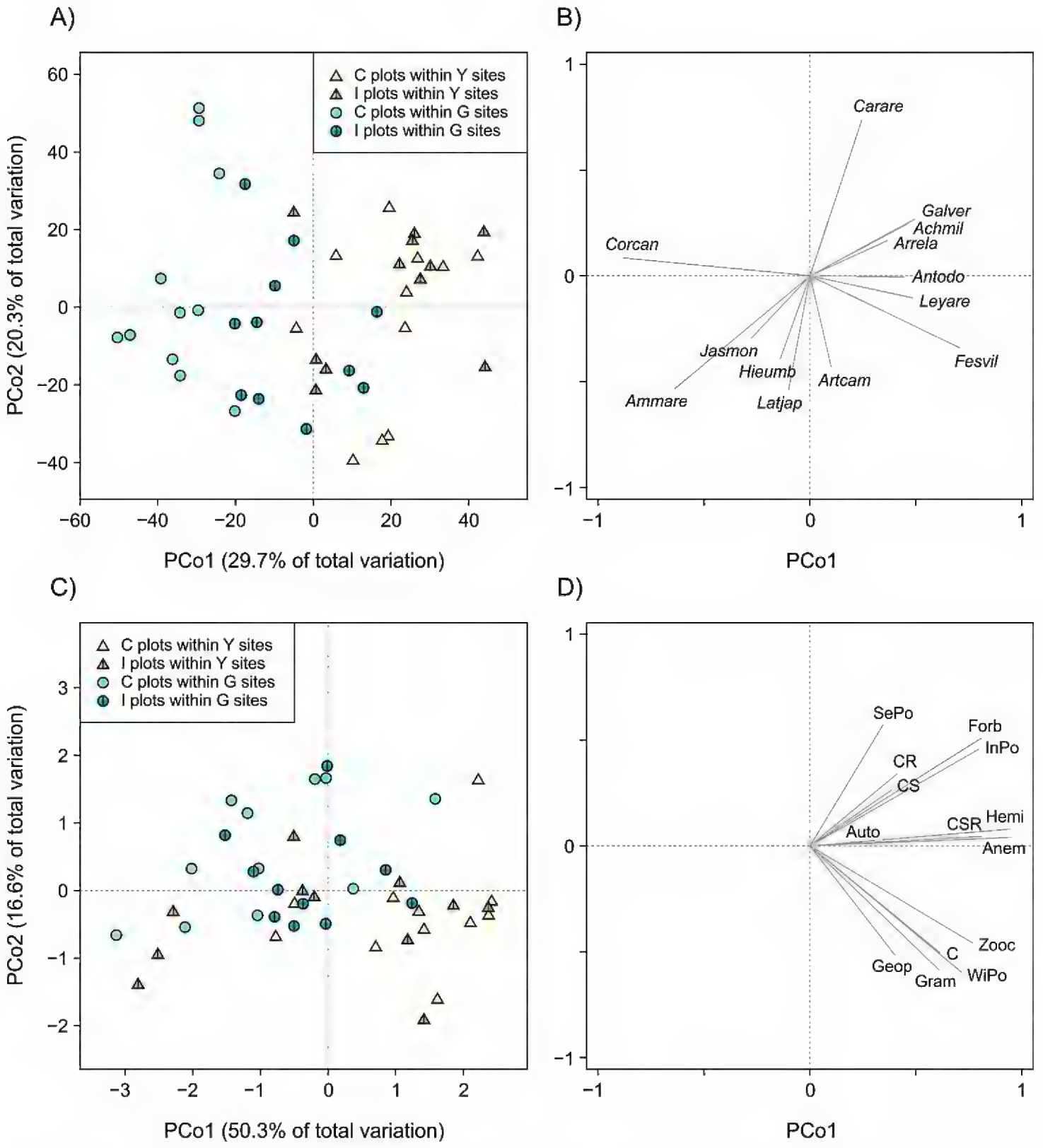

Figure 3. The results of principal coordinates analysis (PCoA) for resident plant species (**A, B**) and functional trait (**C, D**) data. PCoAs were based on Bray-Curtis and Euclidean distances, respectively. The left diagrams (**A, C**) show the position of C (control) and I (invasion) plots established within the Y (yellow dune) and G (grey dune) sites in the ordination space. The right diagrams (**B, D**) show the projection of species (**B**) and functional traits (**D**) on to the ordination space; for clarity, only species that correlated best ($r > 0.4$) with the PCoA axes were displayed. Explanation of acronyms of species names: *Achmil* – *Achillea millefolium*, *Ammare* – *Ammophila arenaria*, *Antodo* – *Anthoxanthum odoratum*, *Arrela* – *Arrhenatherum elatius*, *Artcam* – *Artemisia campestris* ssp. *sericea*, *Carare* – *Carex arenaria*, *Corcan* – *Corynephorus canescens*, *Fesvil* – *Festuca villosa*, *Galver* – *Galium verum*, *Hieumb* – *Hieracium umbellatum* var. *dunense*, *Jasmon* – *Jasione montana* var. *litoralis*, *Latjap* – *Lathyrus japonicus* ssp. *maritimus*, *Leyare* – *Leymus arenarius*. Explanation of functional trait acronyms: Forb – forbs, Gram – graminoids, C – competitors, CR – competitive ruderals, CS – stress-tolerant competitors, CSR – mixed strategists, Geop – geophytes, Hemi – hemicryptophytes, InPo – insect-pollinated, SePo – self-pollinated, WiPo – wind-pollinated, Anem – anemochores, Auto – autochores, Zooc – zoochores.

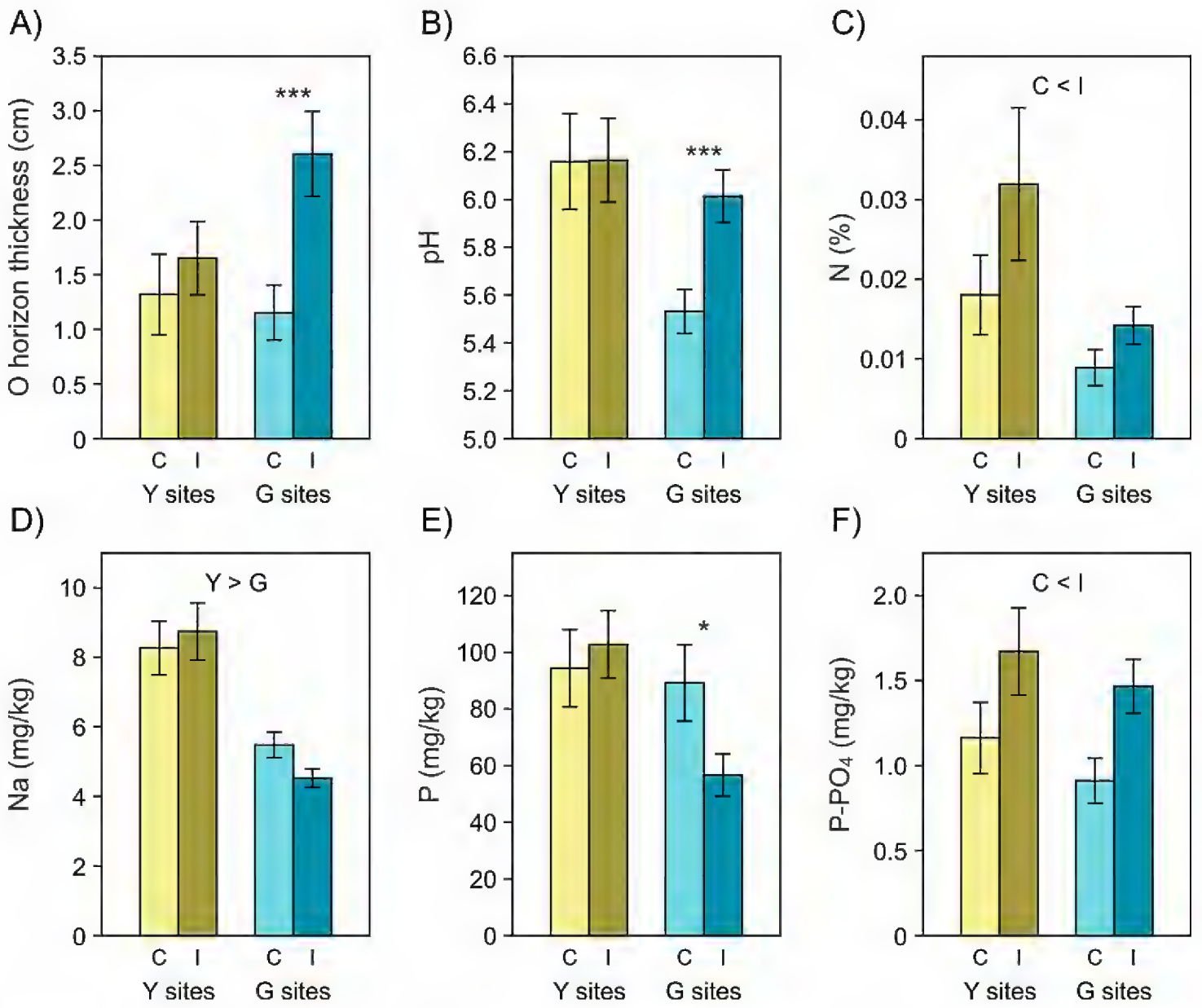

Figure 4. Means and standard errors of selected soil properties calculated for the C (control) and I (invasion) plots within the Y (yellow dune) and G (grey dune) sites. Where a significant site type × plot type interaction was found (see Table 2), the differences between plot types were examined separately for the two types of sites (using Tukey's test) and marked with asterisks (*** $p < 0.001$, * $p < 0.05$). In the remaining cases, inequality signs were used to indicate significant main effects.

number of competitors, hemicryptophytes, insect-pollinated plants, anemochores and zoochores between plot types contributed the most to the interaction effect. Within the grey dune sites, these groups of species were more numerous in the invasion plots than in the control plots, while, within the yellow dune sites, the opposite was true.

According to PERMANOVA, the two types of plots differ in soil properties and these differences depend on the type of site (as evidenced by the site type × plot type interaction; Table 3); they are statistically significant within the grey dune sites ($t = 2.0$, $p = 0.010$) and insignificant within the yellow dune sites ($t = 1.1$, $p = 0.316$). Univariate tests (Table 2) show that the following variables may have contributed to this result: 1) organic layer thickness and pH, which, within the grey dune sites, were higher in the invasion plots than in the control plots (Fig. 4A, B), 2) total N and P-PO_4, which had a similar pattern, but present in both types of sites (Fig. 4C, F) and 3) total P, which within the grey dune sites was higher in the control plots than in the invasion plots (Fig. 4E).

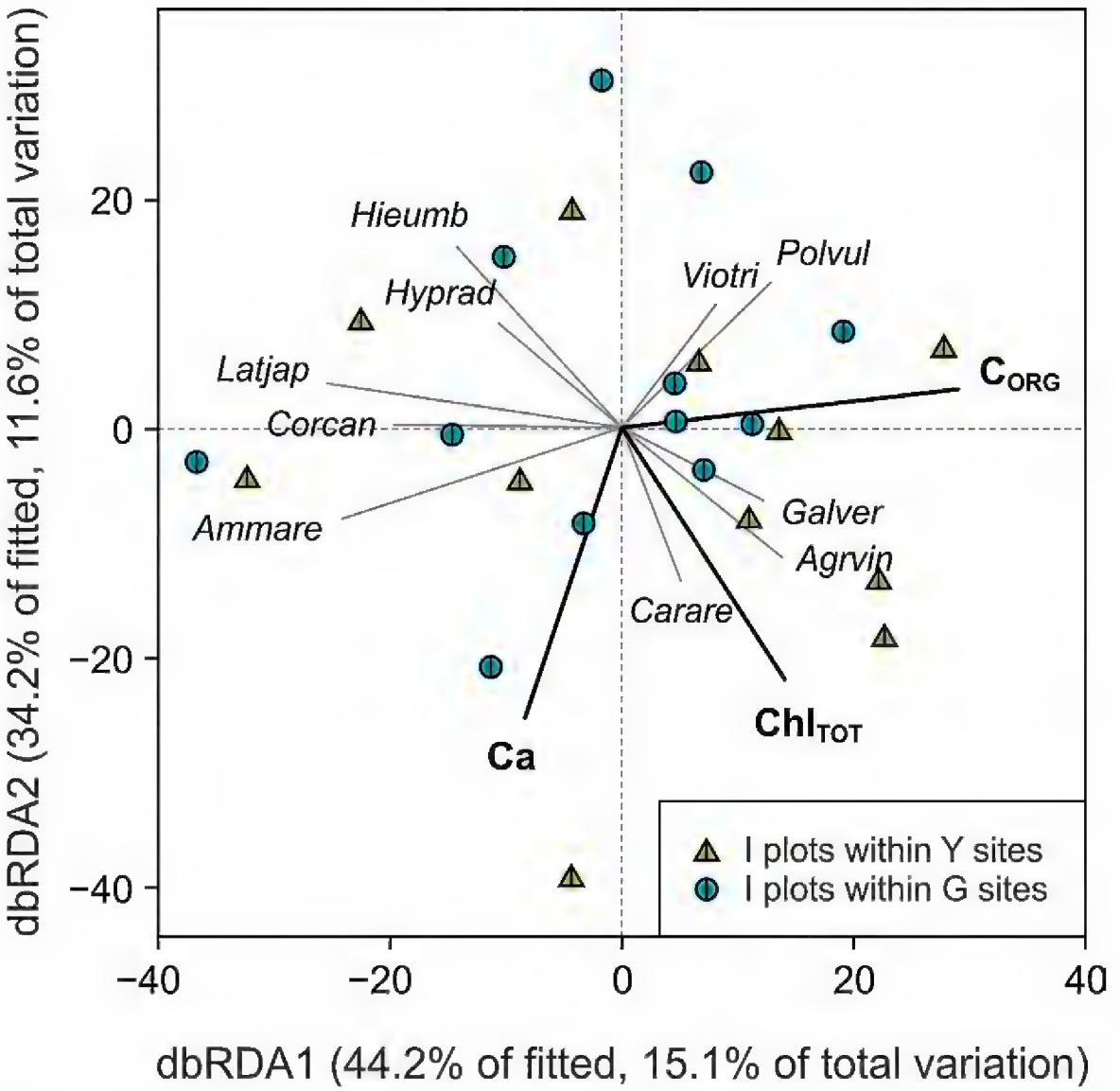

Figure 5. The results of distance-based redundancy analysis (dbRDA) showing the relationship between forward-selected plot characteristics – Ca (soil total Ca), C_{ORG} (soil organic C) and Chl_{TOT} (*Rosa rugosa* leaf total chlorophyll) – and resident plant species occurrence in the invasion plots. The analysis was based on Bray-Curtis distances. Explanation of acronyms of species names: *Agrvin* – *Agrostis vinealis*, *Ammare* – *Ammophila arenaria*, *Carare* – *Carex arenaria*, *Corcan* – *Corynephorus canescens*, *Galver* – *Galium verum*, *Hieumb* – *Hieracium umbellatum* var. *dunense*, *Hyprad* – *Hypochoeris radicata*, *Latjap* – *Lathyrus japonicus* ssp. *maritimus*, *Polvul* – *Polypodium vulgare*, *Viotri* – *Viola tricolor* ssp. *curtisii*

Out of 11 pre-selected habitat variables (four parameters of *R. rugosa* thickets and seven soil physicochemical properties), the DistLM analysis selected three that significantly explained the species composition of resident plants in invaded plots; they were total chlorophyll content in *R. rugosa* leaves (pseudo-F = 2.7, p = 0.012) and the soil contents of organic C (pseudo-F = 3.2, p = 0.001) and total Ca (pseudo-F = 2.7, p = 0.007). The dbRDA diagram (Fig. 5) shows that most species were negatively related to these variables. Total *R. rugosa* leaf chlorophyll was an important explanatory variable in models for total coverage (pseudo-F = 6.4, p = 0.018) and species richness (pseudo-F = 11.7, p = 0.002) of resident plants; it was negatively related to both dependent variables. Other explanatory variables included in these models were total Ca and $N\text{-}NH_4$; the former was positively related to total coverage (pseudo-F = 4.8, p = 0.044) and the latter to species richness (pseudo-F = 5.7, p = 0.030).

Discussion

Non-invaded open dune vegetation

The coastal sand dune system includes dunes at various stages of development, from young, just forming, to mature, fixed dunes (McLachlan and Defeo 2018). They create a spatial gradient of habitat conditions running approximately inland from the shoreline. Ideally, such a gradient extends widely and covers a set of plant community types representing subsequent stages of dune ecological succession – from pioneering communities to forest communities (Peyrat and Fichtner 2011; Doody 2013; McLachlan and Defeo 2018). On the Hel Peninsula, where our study was conducted, the above gradient is relatively short. This is due to the narrowness of the land (most of the Peninsula is less than 1 km wide) and its anthropogenic transformations – the inner dunes were stabilised mainly by Scots pine afforestations, while those closest to the sea shore, especially near the beach entrances, were planted with species of grasses and shrubs, including *R. rugosa* (Mankowski 1906; Łabuz 2013). As a result, the strip of spontaneous open dune vegetation is strongly narrowed and usually dominated at a given place by one of its types: in the western part of the Peninsula, i.e. in an area with high geomorphological dynamics, yellow dune vegetation prevails, while in the eastern part of the peninsula, i.e. in an area with more stabilised landforms, grey dune vegetation is more common (note that this situation is reflected in the distribution of study sites; Fig. 1).

Despite the significant geographical separation between the two types of sites, the studied communities had some common features. They shared several plant species that are important components of dune grassland ecosystems, such as *Ammophila arenaria*, *Artemisia campestris* ssp. *sericea*, *Carex arenaria*, *Corynephorus canescens*, *Festuca villosa*, *Hieracium umbellatum* var. *dunense*, *Lathyrus japonicus* ssp. *maritimus* and *Leymus arenarius*. Moreover, they developed on substrates with very similar physicochemical properties. The yellow dune soils differed from the grey dune soils only in pH and Na content. These parameters were higher for the former, which is a typical result of more intense coastal deposition (sea spray, fresh sand, remains of marine organisms, for example, shells) in places closer to the sea (Hundt 1985; Isermann 2005; Ogura and Yura 2008; Rajaniemi and Allison 2009; McLachlan and Defeo 2018).

Regarding the dissimilarities between the studied communities, they were more obvious than the similarities. Firstly, there were many species present in yellow dune communities, but absent in grey dune communities. This translated into a significantly higher species richness and total plant cover in the former. Secondly, shared species usually showed strong affinities for one type of community, as evidenced by records of their frequencies and abundances (Suppl. material 1: table S1). For example, *Hieracium umbellatum* var. *dunense* was common in both types of communities, but only in yellow dune communities did it reach high cover values; in contrast, *Corynephorus canescens* was always present and abundant on grey dunes, while on yellow dunes, it was observed only twice. The clear separation of points representing the two types of

non-invaded (control) plots in the PCoA diagrams (Fig. 3A, C) confirms the significance of the between-community qualitative differences.

When selecting the yellow and grey dune sites for this study, we identified their vegetation as belonging to the *Ammophiletea* class and the *Koelerio glaucae-Corynephoretea canescentis* class, respectively. In the paper by Peyrat and Fichtner (2011), who surveyed dune vegetation of the southern Baltic coast, communities representing the latter class were generally more species-rich than those representing the former class. This is the opposite of our case. The probable reason for this discrepancy is that our communities are, in fact, late succession sub-stages of the above-mentioned classes. In other words, the yellow dune vegetation in this study should be classified as belonging to the *Elymo-Ammophiletum arenariae festucetosum* subassociation (Matuszkiewicz 2013), which is closely related to the grey dune vegetation. Similarly, the grey dune vegetation, being influenced by nearby Scots pine forest, is to some extent close to the species-poorer vegetation of brown dunes. The discrepancy may also result from the fact that, when calculating the total species richness of dune communities, Peyrat and Fichtner (2011) included vascular plants, bryophytes and lichens, while in our study, the latter two groups – known to be more abundant in grey dunes than in yellow dunes (Isermann 2008b; Peyrat and Fichtner 2011) – were not surveyed.

Invasion-induced changes in open dune vegetation and soil

The plots invaded by *R. rugosa* differed significantly from the non-invaded plots in terms of resident vegetation characteristics. The strong interaction effect, omnipresent in the results of the statistical analyses, indicates that the nature of these differences depended on the type of plant community or, more broadly, the stage of the dune succession. The impact of *R. rugosa* on the quantitative parameters of resident plant communities, i.e. the total cover and species richness, turned out to be fully in line with our expectations: it was negative, but only visible within the yellow dunes. A probable explanation for this phenomenon is that the species of the early succession stages adapt primarily to the challenges of the abiotic environment and not to intense interspecific competition for resources (Olff et al. 1993; Callaway and Walker 1997). As such, they stand no chance against invaders, such as *R. rugosa*, which are strong competitors and, at the same time, perform well in harsh environmental conditions (Bruun 2005). The same cannot be said for the species of the later stages of succession. They have a greater ability to compete, as evidenced by the very fact that they are able to replace existing species in the course of succession (note that quantitative parameters of the grey dune resident vegetation did not decline as a result of invasion; in the case of species richness, the tendency was even the opposite).

The compositional shift in the resident vegetation was another effect of the *R. rugosa* invasion. It was limited to the grey dune community and resulted from significant declines in the frequency and abundance of its two important components, *Corynephorus canescens* and *Ammophila arenaria* and a marked increase in the presence of *Festuca villosa*. The observed response of *Festuca villosa* to the invasion is quite an

intriguing phenomenon. This salt-tolerant grass is adapted to pioneer unstable sandy ground and is, therefore, abundant in yellow dune communities. However, being sensitive to competition, it disappears from these communities when invaded. Thickets of *R. rugosa* in the grey dune habitat theoretically offer even less favourable conditions for *Festuca villosa*, yet our field records show quite the opposite; *Festuca villosa* is a constant component of this community (cf. Suppl. material 1: table S1). This dual behaviour of *Festuca villosa* may be due to the presence of some ecotypic variation across populations of this plant in the study area – one ecotype typically occurs on the early succession dunes and the other in more closed habitats. This supposition is supported by the fact that *Festuca villosa* (synonym: = *Festuca rubra* ssp. *arenaria*) belongs to *Festuca rubra* agg., which is an ecologically diverse grassland-forest taxon, known for its innate adaptability to different environmental conditions (Rozema et al. 1978; Rhebergen and Nelissen 1985; Dąbrowska 2011). The consequence of this reasoning is that *R. rugosa* accelerates ecological succession in grey dunes by facilitating the entry of "forest" plants into the area of originally grassland vegetation. A slight increase in the presence of *Polypodium vulgare* (which is essentially a forest species) in the invaded grey dune communities is in line with the above conclusion.

R. rugosa, as a potential transformer species, may affect resident vegetation indirectly by changing habitat conditions. We expected the direction and magnitude of such changes to be similar for both types of dunes, with more pronounced community-level consequences in the case of yellow dunes (since plant communities of the early stages of succession function under a shortage and sometimes excess, of many resources, they may be more susceptible to fluctuations in their level than communities of milder environments). The obtained results did not confirm this hypothesis. Only two of the measured soil parameters (total N and phosphate contents) changed as expected both in the yellow and grey dunes (they increased under *R. rugosa*), without, however, causing a clear response of resident plants (for example, in form of the appearance of nutrient-demanding species). The remaining soil parameters either did not differ between the invasion and control plots or they differed only within the grey dune sites. Amongst the latter, noteworthy is the thickness of the organic layer, which doubled in the invasion plots. Varying wind exposure likely contributed to this pattern. Grey dunes are located further from the sea, in places sheltered on one side by other dunes and, on the other, by forest, which translates into less intensive blowing of the litter produced by *R. rugosa* and faster accumulation of organic matter in the soil. Perhaps this is part of the mechanism that facilitates brown dune species entry into the grey dune communities discussed above.

Open dune vegetation response to the variability of invader thickets

A meta-analysis of data from observational studies and experimental manipulations clearly showed that the competitive pressure of the invasive species is a function of its abundance (Sofaer et al. 2018; Bradley et al. 2019). Regardless of the shape of this function, it can be expected that the negative impact of invasion on resident communities

will initially increase, that is, as the invader spreads. However, after a longer period of time, this time-impact relationship may become weaker or even reversed, as demonstrated in the review by Strayer et al. (2006). The reasons for this phenomenon can be both external and internal. The former includes changes in the biological community and/or the abiotic environment, for example, the emergence and proliferation of pathogens or predators (Fan et al. 2016: Flory et al. 2018) and the latter changes in the invader, for example, its ageing (Staska et al. 2014). Both may reduce the density and vigour of the invader, thus facilitating the recovery of resident species.

R. rugosa is a perennial plant, so it is common to find individuals representing different ontogenetic stages within the area of invasion. At the latest stage, when the plant ages, dead shoots appear and, with them, gaps in the canopy. We expected that the resulting reduced competitive pressure would have a positive effect on the occurrence of resident plants. However, we did not observe any relationship between the variables reflecting the developmental stages of *R. rugosa* (in particular, the percentage of dead shoots) and the quantitative and qualitative parameters of the resident plant community. It is possible that the sampling criteria adopted in the study contributed to this result. The plots were established more or less in the middle of the *R. rugosa* patches, i.e. in their older parts, thus excluding the younger specimens, which dominated at the edges, i.e. at the front of the invasion. Consequently, the ontogenetic variation of *R. rugosa* could not be fully captured.

Interestingly, the total content of chlorophyll in *R. rugosa* leaves turned out to be an important explanatory factor for the resident plant community parameters. Regardless of the type of dune, its low values were usually accompanied by high cover and species richness of resident vegetation, as well as more abundant occurrence of species characteristics of dune grassland communities. The chlorophyll content is considered an indicator of a plant's nutrient supply or exposure to environmental stresses (Zhang et al. 2022). Therefore, the result suggests that there is a gradient of habitat severity within both the yellow and grey dune sites affecting *R rugosa*. Even if this gradient is not visible in the abundance of the invader, it is reflected in its condition (and, thus, in its competitive potential), which creates an opportunity for resident vegetation to recover.

Conclusions

R. rugosa readily invades both yellow and grey dune communities on the Baltic coast. Significantly, although these communities are closely related and often occur next to each other (they represent two adjacent stages of ecological succession), *R. rugosa* affects them in a radically different way. In yellow dune sites, it outcompetes most of the resident plant species, which is reflected in substantial declines in their total cover and richness. Given that there are virtually no changes in soil properties due to invasion, the underlying mechanism is likely to include only direct effects, such as space takeover and shading. In grey dune sites, *R. rugosa* causes a shift in the species composition,

without altering the quantitative parameters of the resident community. Contrary to the yellow dune situation, the presence of *R. rugosa* has a significant impact on the soil – the litter it produces can accumulate (because the grey dune habitat is less exposed to the wind), thus creating a solid organic layer. Shading (direct effect) and habitat transformation (indirect effect) appear to promote plants of brown dunes (for example, shade-tolerant ecotype of *Festuca villosa*, *Polygonum vulgare*), which means that the *R. rugosa* invasion of grey dunes accelerates their ecological succession. Finally, the effect of invasion depends not only on the type of habitat, but also on the invader itself. When the condition of the invader is degraded, for example, as a result of environmental stresses, there is an opportunity for resident plants to recover.

The above findings confirm the main hypothesis put forward in this paper, namely that the influence of *R. rugosa* on local vegetation and soil is modified by the ecological context. This context should be taken into account when, for example, invader removal measures are planned. It seems that such measures could bring better results in the yellow dunes. Firstly, because *R. rugosa* does not significantly change soil properties in this habitat. Secondly, mechanical disturbances to the soil profile that occur when removing invasive plants are probably of little importance in a situation where the soil surface is not stabilised anyway. In the case of grey dunes, in addition to removing the invader, it may also be necessary to remove excess organic matter. Moreover, measure-induced disturbances are likely to alter the nature of this habitat with unpredictable consequences for the ecosystem.

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References

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth, 214 pp.

Barnes JD, Balaguer L, Manrique E, Elvira S, Davison AW (1992) A reappraisal of the use of DMSO for the extraction and determination of chlorophylls *a* and *b* in lichens and higher plants. Environmental and Experimental Botany 32(2): 85–100. https://doi.org/10.1016/0098-8472(92)90034-Y

Belcher CR (1977) Effect of sand cover on the survival and vigor of *Rosa rugosa* Thunb. International Journal of Biometeorology 21(3): 276–280. https://doi.org/10.1007/BF01552881

Boege K, Marquis RJ (2006) Plant quality and predation risk mediated by plant ontogeny: Consequences for herbivores and plants. Oikos 115(3): 559–572. https://doi.org/10.1111/j.2006.0030-1299.15076.x

Borges LL, Alves SF, Sampaio BL, Conceição EC, Bara MTF, Paula JR (2013) Environmental factors affecting the concentration of phenolic compounds in *Myrcia tomentosa* leaves. Revista Brasileira de Farmacognosia 23: 230–238. https://doi.org/10.1590/S0102-695X2013005000019

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance-impact relationship for invasive species. Proceedings of the National Academy of Sciences of the United States of America 116(20): 9919–9924. https://doi.org/10.1073/pnas.1818081116

Bruun HH (2005) *Rosa rugosa* Thunb. ex Murray. Journal of Ecology 93(2): 441–470. https://doi.org/10.1111/j.1365-2745.2005.01002.x

CABI (2022) *Rosa rugosa*. Invasive Species Compendium. CAB International, Wallingford. www.cabi.org/isc [October 25, 2022]

Callaway RM, Walker LR (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78(7): 1958–1965. https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18(1): 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Dąbrowska A (2011) Variability of morphological and anatomical traits in natural populations of *Festuca rubra* and *F. nigrescens*. Acta Agrobotanica 64(4): 159–170. https://doi.org/10.5586/aa.2011.057

Dassonville N, Vanderhoeven S, Vanparys V, Hayez M, Gruber W, Meerts P (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia 157(1): 131–140. https://doi.org/10.1007/s00442-008-1054-6

Doody JP (2013) Sand Dune Conservation, Management and Restoration. Springer, Dordrecht, 306 pp. https://doi.org/10.1007/978-94-007-4731-9

Fan S, Yu H, Dong X, Wang L, Chen X, Yu D, Liu C (2016) Invasive plant *Alternanthera philoxeroides* suffers more severe herbivory pressure than native competitors in recipient communities. Scientific Reports 6(1): e36542. https://doi.org/10.1038/srep36542

Fei S, Phillips J, Shouse M (2014) Biogeomorphic impacts of invasive species. Annual Review of Ecology, Evolution, and Systematics 45(1): 69–87. https://doi.org/10.1146/annurev-ecolsys-120213-091928

Flory SL, Alba C, Clay K, Holt RD, Goss EM (2018) Emerging pathogens can suppress invaders and promote native species recovery. Biological Invasions 20(1): 5–8. https://doi.org/10.1007/s10530-017-1438-9

Fox J, Weisberg S (2011) An R Companion to Applied Regression (2nd edn.). Sage, Thousand Oaks.

Fried G, Carboni M, Mahaut L, Violle C (2019) Functional traits modulate plant community responses to alien plant invasion. Perspectives in Plant Ecology, Evolution and Systematics 37: 53–63. https://doi.org/10.1016/j.ppees.2019.02.003

Helsen K, Matsushima H, Somers B, Honnay O (2021) A trait-based approach across the native and invaded range to understand plant invasiveness and community impact. Oikos 130(6): 1001–1013. https://doi.org/10.1111/oik.08034

Huang WZ, Schoenau JJ (1998) Fluxes of water-soluble nitrogen and phosphorus in the forest floor and surface mineral soil of a boreal aspen stand. Geoderma 81(3–4): 251–264. https://doi.org/10.1016/S0016-7061(97)00092-X

Hundt R (1985) Phytosociological and ecological aspects of the dunes on the Isle of Rügen, Baltic sea. Vegetatio 61(1–3): 97–103. https://doi.org/10.1007/BF00039814

Isermann M (2005) Soil pH and species diversity in coastal dunes. Plant Ecology 178(1): 111–120. https://doi.org/10.1007/s11258-004-2558-8

Isermann M (2008a) Classification and habitat characteristics of plant communities invaded by the non-native *Rosa rugosa* Thunb. in NW Europe. Phytocoenologia 38(1–2): 133–150. https://doi.org/10.1127/0340-269X/2008/0038-0133

Isermann M (2008b) Effects of *Rosa rugosa* invasion in different coastal dune vegetation types. In: Tokarska-Guzik B, Brock JH, Brundu G, Child L, Daehler CC, Pyšek P (Eds) Plant Invasions: Human Perception, Ecological Impacts and Management. Backhuys Publishers, Leiden, 289–306.

ISO (1994) Soil quality – Determination of pH (ISO Standard No. 10390). International Organization for Standardization, Genève.

ISO (1995) Soil quality – Determination of organic and total carbon after dry combustion (elementary analysis) (ISO Standard No. 10694). International Organization for Standardization, Genève.

IUSS Working Group WRB (2015) World Reference Base for Soil Resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome, 192 pp.

Kaushik P, Pati PK, Khan ML, Khare PK (2022) Plant functional traits best explain invasive species' performance within a dynamic ecosystem – A review. Trees, Forests and People 8: e100260. https://doi.org/10.1016/j.tfp.2022.100260

Kaźmierczakowa R, Bloch-Orłowska J, Celka Z, Cwener A, Dajdok Z, Michalska-Hejduk D, Pawlikowski P, Szczęśniak E, Ziarnek K (2016) Polish Red List of Pteridophytes and Flowering Plants. Institute of Nature Conservation, Polish Academy of Science, Kraków, 44 pp.

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: A database of life-history traits of the Northwest European flora. Journal of Ecology 96(6): 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz S, Kühn I, Durka W (2002) BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Bundesamt für Naturschutz, Bonn, 334 pp.

Kollmann J, Frederiksen L, Vestergaard P, Bruun HH (2007) Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. Biological Invasions 9(1): 31–42. https://doi.org/10.1007/s10530-006-9003-y

Kollmann J, Jørgensen RH, Roelsgaard J, Skov-Petersen H (2009) Establishment and clonal spread of the alien shrub *Rosa rugosa* in coastal dunes – A method for reconstructing and predicting invasion patterns. Landscape and Urban Planning 93(3–4): 194–200. https://doi.org/10.1016/j.landurbplan.2009.07.006

Kollmann J, Brink-Jensen K, Frandsen SI, Hansen MK (2011) Uprooting and burial of invasive alien plants: A new tool in coastal restoration? Restoration Ecology 19(3): 371–378. https://doi.org/10.1111/j.1526-100X.2009.00569.x

Kunttu P, Kunttu S-M (2017) Distribution and habitat preferences of the invasive alien *Rosa rugosa* (Rosaceae) in Archipelago Sea National Park, SW Finland. Polish Botanical Journal 62(1): 99–115. https://doi.org/10.1515/pbj-2017-0009

Łabuz TA (2013) Polish coastal dunes – affecting factors and morphology. Landform Analysis 22: 33–59. https://doi.org/10.12657/landfana.022.004

Lichtenthaler HK, Buschmann C, Knapp M (2004) Measurement of chlorophyll fluorescence kinetics (Kautsky effect) and the chlorophyll fluorescence decrease ratio (RFd–values) with the PAM-Fluorometer. In: Filek N, Biesaga-Kościelniak J, Marcińska I (Eds) Analytical methods in plant stress biology. The Franciszek Gorski Institute of Plant Physiology of the Polish Academy of Sciences, Kraków, 93–111.

Lundgren MR, Des Marais DL (2020) Life history variation as a model for understanding trade-offs in plant–environment interactions. Current Biology 30(4): R180–R189. https://doi.org/10.1016/j.cub.2020.01.003

Mankowski H (1906) Die Halbinsel Hela. Verlag und Druck von A. W. Kafemann, Danzig, 69 pp.

Matuszkiewicz W (2013) Przewodnik do Oznaczania Zbiorowisk Roślinnych Polski. Wydawnictwo Naukowe PWN, Warszawa, 540 pp.

McLachlan A, Defeo O (2018) The Ecology of Sandy Shores. Academic Press, London, 572 pp. https://doi.org/10.1016/B978-0-12-809467-9.00013-8

Ministry of Environment of the Republic of Poland (2014) Regulation of the Minister of the Environment of 9 October 2014 on the protection of plant species. Polish Journal of Laws, item 1409.

Mirek Z, Piękoś-Mirkowa H, Zając A, Zając M (2002) Flowering Plants and Pteridophytes of Poland – a Checklist. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 442 pp.

Nakata Y, Hioki Y, Oguchi T (2018) Evaluation of beach vegetation for conservation/rehabilitation in Tottori Prefecture, Southwest Japan. Landscape and Ecological Engineering 14(2): 231–243. https://doi.org/10.1007/s11355-017-0344-8

Nowosielski O (1974) Metody Oznaczania Potrzeb Nawożenia. Panstwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 91 pp.

Ogura A, Yura H (2008) Effects of sandblasting and salt spray on inland plants transplanted to coastal sand dunes. Ecological Research 23(1): 107–112. https://doi.org/10.1007/s11284-007-0347-2

Olff H, Huisman J, Van Tooren BF (1993) Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. Journal of Ecology 81(4): 693–706. https://doi.org/10.2307/2261667

Perzanowska J, Korzeniak J (2020) Red list of Natura 2000 habitat types of Poland. Journal for Nature Conservation 56: e125834. https://doi.org/10.1016/j.jnc.2020.125834

Peyrat J, Fichtner A (2011) Plant species diversity in dry coastal dunes of the southern Baltic coast. Community Ecology 12(2): 220–226. https://doi.org/10.1556/ComEc.12.2011.2.10

Pickart AJ (2021) *Ammophila* invasion ecology and dune restoration on the West Coast of North America. Diversity 13(12): e629. https://doi.org/10.3390/d13120629

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: Linear and nonlinear mixed effects models. R package ver. 3.1-131. https://CRAN.R-project.org/package=nlme [July 10, 2017]

PN-ISO (1997) Jakość Gleby – Oznaczanie Przewodności Elektrycznej Właściwej (Standard nr 11265). Polski Komitet Normalizacyjny, Warszawa.

Qiu T, Aravena M-C, Andrus R, Ascoli D, Bergeron Y, Berretti R, Bogdziewicz M, Boivin T, Bonal R, Caignard T, Calama R, Camarero JJ, Clark CJ, Courbaud B, Delzon S, Donoso Calderon S, Farfan-Rios W, Gehring CA, Gilbert GS, Greenberg CH, Guo Q, Hille Ris Lambers J, Hoshizaki K, Ibanez I, Journé V, Kilner CL, Kobe RK, Koenig WD, Kunstler G, LaMontagne JM, Ledwon M, Lutz JA, Motta R, Myers JA, Nagel TA, Nuñez CL, Pearse IS, Piechnik Ł, Poulsen JR, Poulton-Kamakura R, Redmond MD, Reid CD, Rodman KC, Scher CL, Schmidt Van Marle H, Seget B, Sharma S, Silman M, Swenson JJ, Swift M, Uriarte M, Vacchiano G, Veblen TT, Whipple AV, Whitham TG, Wion AP, Wright SJ, Zhu K, Zimmerman JK, Żywiec M, Clark JS (2021) Is there tree senescence? The fecundity evidence. Proceedings of the National Academy of Sciences of the United States of America 118(34): e2106130118. https://doi.org/10.1073/pnas.2106130118

R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Rajaniemi TK, Allison VJ (2009) Abiotic conditions and plant cover differentially affect microbial biomass and community composition on dune gradients. Soil Biology & Biochemistry 41(1): 102–109. https://doi.org/10.1016/j.soilbio.2008.10.001

Rhebergen LJ, Nelissen HJM (1985) Ecotypic differentiation within *Festuca rubra* L. occurring in a heterogeneous coastal environment. Vegetatio 61(1–3): 197–202. https://doi.org/10.1007/BF00039825

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity & Distributions 6(2): 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Rozema J, Rozema-Dijst E, Freijsen AHJ, Huber JJL (1978) Population differentiation within *Festuca rubra* L. with regard to soil salinity and soil water. Oecologia 34(3): 329–341. https://doi.org/10.1007/BF00344910

Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. Ecosphere 9(9): e02415. https://doi.org/10.1002/ecs2.2415

Staska B, Essl F, Samimi C (2014) Density and age of invasive *Robinia pseudoacacia* modulate its impact on floodplain forests. Basic and Applied Ecology 15(6): 551–558. https://doi.org/10.1016/j.baae.2014.07.010

Stefanowicz AM, Zubek S, Stanek M, Grześ IM, Rożej-Pabijan E, Błaszkowski J, Woch MW (2019) Invasion of *Rosa rugosa* induced changes in soil nutrients and microbial communities of coastal sand dunes. The Science of the Total Environment 677: 340–349. https://doi.org/10.1016/j.scitotenv.2019.04.408

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21(11): 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Tamary E, Nevo R, Naveh L, Levin-Zaidman S, Kiss V, Savidor A, Levin Y, Eyal Y, Reich Z, Adam Z (2019) Chlorophyll catabolism precedes changes in chloroplast structure and proteome during leaf senescence. Plant Direct 3(3): e00127. https://doi.org/10.1002/pld3.127

Thiele J, Isermann M, Kollmann J, Otte A (2011) Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity. NeoBiota 10: 65–79. https://doi.org/10.3897/neobiota.10.1191

Tichý L, Hennekens SM, Novák P, Rodwell JS, Schaminée JHJ, Chytrý M (2020) Optimal transformation of species cover for vegetation classification. Applied Vegetation Science 23(4): 710–717. https://doi.org/10.1111/avsc.12510

Tomczak A (1995) Relief, geology and evolution of the Hel Spit. Journal of Coastal Research 22(Spec. Issue): 181–185.

Tuominen A, Salminen J-P (2017) Hydrolyzable tannins, flavonol glycosides, and phenolic acids show seasonal and ontogenic variation in *Geranium sylvaticum*. Journal of Agricultural and Food Chemistry 65(31): 6387–6403. https://doi.org/10.1021/acs.jafc.7b00918

Van De Walle R, Massol F, Vandegehuchte ML, Bonte D (2022) The distribution and impact of an invasive plant species (*Senecio inaequidens*) on a dune building engineer (*Calamagrostis arenaria*). NeoBiota 72: 1–23. https://doi.org/10.3897/neobiota.72.78511

Vanderhoeven S, Dassonville N, Meerts P (2005) Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. Plant and Soil 275(1–2): 169–179. https://doi.org/10.1007/s11104-005-1257-0

Vetter VMS, Tjaden NB, Jaeschke A, Buhk C, Wahl V, Wasowicz P, Jentsch A (2018) Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity. Frontiers in Plant Science 9: e715. https://doi.org/10.3389/fpls.2018.00715

Yang J-H, Zhang S-P, Liu J, Zhai W, Wang R-Q (2009) Genetic diversity of the endangered species *Rosa rugosa* Thunb. in China and implications for conservation strategies. Journal of Systematics and Evolution 47(6): 515–524. https://doi.org/10.1111/j.1759-6831.2009.00049.x

Zhang H, Ge Y, Xie X, Atefi A, Wijewardane NK, Thapa S (2022) High throughput analysis of leaf chlorophyll content in sorghum using RGB, hyperspectral, and fluorescence imaging and sensor fusion. Plant Methods 18(1): 1–60. https://doi.org/10.1186/s13007-022-00892-0

Supplementary material 1

Detailed information and results of supplementary analyses on the structure of resident plant communities

Authors: Marcin W. Woch, Paweł Kapusta, Małgorzata Stanek, Katarzyna Możdżeń, Irena M. Grześ, Elżbieta Rożej-Pabijan, Anna M. Stefanowicz

Data type: occurrences, statistics

Explanation note: Venn diagram showing the number of species exclusive for and shared between four types of plots: yellow dune control and invasion plots and grey dune control and invasion plots. Table showing species shared between and exclusive for four types of plots – yellow dune control and invasion plots and grey dune control and invasion plots – with their frequency and average percentage coverage. Table showing resident plant species that contribute most to the dissimilarity between control and invasion plots according to the SIMPER analysis. Table showing resident plant functional traits for the control and invasion plots within the yellow and grey dune sites, and the effects of site type, plot type and their interaction on these properties, as shown by F-values derived from the LME analysis.

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